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Transpiration of cottonwood/willow forest estimated from sap flux

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Abstract

Cottonwood/willow forests in the American Southwest consist of discrete, even-aged vegetation patches arranged in narrow strips along active and abandoned stream channels of alluvial flood plains. We used the heat-pulse velocity technique in this study to estimate transpiration in twelve such forest patches along a perennially flowing reach of the San Pedro River in southeastern Arizona, USA during five periods from April to October, 1997. Transpiration per unit sapwood area was consistently higher for the larger cottonwood trees found on outer secondary channels compared to that of smaller cottonwood trees along the active channel, but statistically significant differences were found only in August and October. Conversely, transpiration per unit sapwood area in willow was markedly higher for trees along the primary channel than for those few larger trees that were sampled on the outer margins of the forest. Average daily transpiration at the canopy scale among the patches in July was 4.8 ±0.7 mm day^{-1} and ranged from 5.7 ±0.6 mm d^{-1} in young forest patches adjacent to the primary stream channel to 3.1 ±0.6 mm d^{-1} in more successionally advanced patches on secondary channels. Differences in our estimates of transpiration between forest patches along primary and secondary stream channels were related to differences in the ratio of sapwood area to ground area of the forest patches, and leaf area index. Estimates of transpiration from this forest type, and projections of transpiration and groundwater flux over larger areas on the San Pedro River, should take into account structural variation in these forests that relate to population dynamics of dominant trees.

Key words: sap flow, transpiration, patch dynamics, forest structure, cottonwood, willow, *Salix goodingii*, *Populus fremontii*

Introduction

Riparian forests of arid and semi-arid regions of western North America are occupied by drought intolerant tree species that rely on shallow groundwater for establishment, growth, and transpiration (Smith et al., 1991; Busch et al., 1992; Stromberg, 1993; Snyder and Williams, this issue). Forests dominated by cottonwood (*Populus*) and willow (*Salix*), for instance, are locally restricted to primary floodplains of rivers, streams, and dry washes where groundwater is no deeper than about five meters (Reichenbacher, 1984; Asplund and Gooch, 1988; Stromberg, 1998). Persistence of these forests depends on disturbance; local regeneration is controlled by flooding that destroys existing vegetation and creates "safe sites" for seedling establishment on scoured and exposed sand bars (Stromberg, 1993). Because of very localized patterns of seedling establishment and bank erosion, cottonwood/willow forests are characteristically comprised of discreet, even-aged "patches" arranged in narrow strips along active and abandoned stream channels (Bradley and Smith, 1985; Johnson, 1994). As forest patches age, they become less dense because of mortality. Eventually these patches become dominated by just a few very large cottonwood and willow individuals (Stromberg, 1998).

Cottonwood/willow forests potentially transpire large quantities of groundwater from channel aquifers. Structural dynamics at local scales in these forests, therefore, may have important ramifications for transpiration at larger scales. It is not known, for instance, if transpiration from these forest patches declines during succession as trees become separated from the active stream channel or if individuals that survive in a patch develop higher transpiration rates due to competitive release. Enhanced growth and gas exchange is commonly observed in trees released from competition following artificial forest thinning (Kozlowski et al. 1991). Linking patch dynamics and transpiration in these forests, therefore, may be useful for modeling catchment-scale hydrologic dynamics in flood plain environments in the Southwest.

There are few estimates of the magnitude or spatial and temporal heterogeneity of transpiration fluxes in arid and semi-arid riparian forests. In particular, the unique structure of southwestern cottonwood/willow forests precludes the use of micrometeorological approaches for transpiration

estimates (but see Hipps et al., 1998). Here we use the heat-pulse velocity (HPV) method to characterize spatial and seasonal variability of transpiration from cottonwood/willow forest in southeastern Arizona as a contribution to the Semi-Arid Land-Surface-Atmosphere (SALSA) program field campaigns in the riparian ecosystem on the San Pedro River (see Goodrich et al., this volume for overview). Estimates of whole-tree transpiration from HPV sensors tend to differ by less than 15% from cut-tree (potometer) measurements (Olbrich, 1991; Smith, 1991; Barret, 1992; Hatton et al., 1995). In homogeneous broad-leaf and coniferous forests, estimates of transpiration from the HPV method agree favorably to estimates from micrometeorological methods such as Bowen ratio and eddy covariance (Kelliher et al., 1992; Loustau et al., 1996; Saugier et al,. 1996).

Since establishment of cottonwood and willow seedlings does not occur beneath existing cottonwood/willow canopies, we hypothesized that transpiration should decline systematically as patches of this vegetation type age and thin. Thus, we predicted that transpiration on a canopy area basis would be lower in forest patches consisting of large trees found on secondary stream channels than in recently established patches along the active primary channels.

Materials and Methods

Study site

Our study was conducted along a perennially flowing reach of the San Pedro River (Lewis Springs study site; 31° 33' N, 110° 07' W; 1250 m elevation) within the San Pedro National Riparian Conservation Area in southeastern Arizona, U.S.A. The riparian forest vegetation consisted of Frémont cottonwood (*Populus fremontii* Wats.) and Gooding willow (*Salix goodingii* Ball) as dominant and sub-dominant overstory species, respectively. Mesquite (*Prosopis velutina* Woot.) and seep-willow (*Baccharis glutinosa* Pers.) formed a sparse woody understory. Patches of cottonwood/willow riparian forest were located along both the primary stream channel and along dry secondary channels.

Heat pulse velocity estimates of transpiration

Heat pulse velocity probes (Thermal Logic Inc., Pullman, WA) were implanted in cottonwood and willow trees of differing diameters proportional to the range of tree basal diameter classes determined from vegetation surveys. Vegetation surveys consisted of four belt transects on each side of the stream channel and extended to the edge of the riparian forest. Transects were 30 m wide and were divided into 10-m long sections. Total counts of individual trees, as well as their corresponding diameters (diameter at approximately 1.35 m height), were recorded for cottonwood and willow.

Transpiration was estimated using the HPV method for five periods during the 1997-growing season: April 20-21, June 6-10, July 10-13, August 11-16, and October 11-16. Nine cottonwood trees were selected with diameters ranging from 0.14 to 0.75 m. Six willow trees were selected with diameters ranging from 0.15 to 0.24 m. Each tree, depending on its diameter, received from three to five probes, placed equidistant around the trunk. Bark was removed until the cambium was exposed and sensors were inserted into holes drilled parallel with the grain of the wood. Before insertion, probes were coated with silicone gel to ensure good thermal contact between probe elements and sapwood. After insertion, exposed cambium was covered with silicone gel to reduce evaporation from the wood

surface, and then covered with aluminum foil to reduce effects of ambient temperature fluctuations and solar radiation.

Four independent data logger (CR10X, Campbell Scientific, Logan UT) and control systems with multiplexors (AM416, Campbell Scientific, Logan UT), relay drivers (A21REL-12, Campbell Scientific, Logan UT), and 12-volt marine batteries were used to generate heat pulses and monitor their travel through the xylem. Eight-second heat pulses were produced by the upstream heating elements. Three downstream thermocouples (at 10, 20, 30 mm depth into the xylem) measured xylem temperature for 60 seconds after initiation of the heat pulse. Sap velocity V (cm h^{-1}) was calculated from Cohen et al. (1981) as:

$$V = r \frac{\sqrt{(1 - t_m / t_{mo})}}{t_{mo}} \tag{1}$$

where r is the distance between heater and thermocouple (6 mm), t_m is time to maximum recorded temperature, and t_{mo} is the time to maximum temperature at zero flow (assumed to be at pre-dawn, 0200 to 0400 h). The heat pulse velocity method has been shown, through numerical analysis, to be less accurate at low sap velocities than at higher sap velocities (Swanson and Whitfield, 1981; Barrett, 1995). Based on conservative calculations from formulas described by Swanson and Whitfield (1981), velocities below 10 cm h^{-1} were ignored and assumed to be zero. Mass flow of sap J (volume per unit time) was calculated from Cohen et al. (1981):

$$J = \frac{\rho c}{\rho_w c_w} \Sigma V_i A_i \tag{2}$$

where ρc and $\rho_w c_w$ are the volumetric specific heats (MJ m^{-3} °C^{-1}) of wet wood and water, respectively. V_i and A_i are the sap velocity and the cross sectional area of the ith increment of sapwood being measured by a thermocouple. The volumetric specific heat of wet wood (ρc) was determined

during the presumed period of zero flow (0200-0400 h) using the relationship for dissipation of a heat

pulse with no fluid correction developed by Campbell et al. (1991):

$$\boldsymbol{rc} = \frac{Q}{(e\boldsymbol{p}r^2 \Delta T_m)} \tag{3}$$

where $\boldsymbol{D}T_m$ is the maximum temperature rise recorded by the thermocouple. Q is the heat input (J m^{-1})

of the heat pulse calculated as:

$$Q = tI^2 \left(\frac{R_h}{L} \right) \tag{4}$$

where t is the heating time ($8s$), I is the heater current, and R_h/L is the resistance per meter of the heater

(in this case, 1141 W m^{-1}). Gravimetric assessment of $\boldsymbol{rc}$ was identical to $\boldsymbol{rc}$ calculated using zero-

flow.

Transpiration (E) was expressed as sap flux on a sapwood area basis. In order to calculate sap

flux (g cm^{2} h^{-1}) for a given tree, J (Eq. 2) was divided by the sapwood area of the tree. The amount of

sapwood area was determined by taking an increment core and discriminating between sapwood and

heartwood based on color differences. By expressing E in terms of sapwood area, all the trees within

the sample area could be directly compared. This final step in calculating E for a single tree normalizes

E with respect to sapwood area.

Heat pulse velocity sensors were compared with temperature difference probes (Dynamax Inc.,

Houston, TX) to gauge the comparative reliability of our estimates. Temperature difference probes

(TDP) use a constant heat balance method to estimate sap flux similar to the method outlined by Granier

(1985, 1987). In June 1997, both probe types were implanted in a single cottonwood tree and sap

flow was recorded for two days. A relatively young tree was chosen for comparison to minimize effects

of probe placement; younger trees generally have uniform grain and xylem structure and are less likely to show positional effects.

Aggregation

Transpiration estimates for different forest patches and the entire stand were derived from scaling of the direct measurements of the amount of water used by individual trees of each species and size class (Kelliher et al., 1992; Hatton et al., 1995; Granier, 1996). Data from the HPV method yielded transpiration in terms of the sapwood area of a given tree.

To relate sapwood area to an easily measured parameter, 19 cottonwood and 29 willow trees were cored and measured for diameter and sapwood area. As stated previously, sharp transitions from lightly colored, apparently active xylem, to darkly colored and water saturated wood was used to distinguish between the sapwood-heartwood boundary. Data for tree diameters from forest patches were then converted to sapwood area using predictive equations generated from regression analysis. Sapwood area estimates were combined with estimates of *E* for aggregation.

Estimation of patch and stand transpiration on a canopy area basis was extrapolated from individual tree sapwood flux using sapwood area for cottonwood and willow and projected canopy area of forest patches. Twelve forest patches were selected representing 5 newly established and 7 successionally advanced patches in which projected canopy area could be assessed digitally using aerial photographs (Fig. 1). The diameter of all cottonwood and willow trees in each patch and the canopy area (m^2) of each patch was measured (Table 1). Combined cottonwood and willow sapwood area of each forest patch was estimated using sapwood area-to-diameter relationships previously developed. Sapwood area of clusters and average *E* (sapwood area basis) calculated from individual trees were used to estimate the total flow of water ($kg\ h^{-1}$) from a forest patch.

Error Estimates of Transpiration

The error associated with estimates of patch and stand level transpiration was a function of the error estimates for each step in the aggregation scheme. The total error for a given patch of riparian vegetation was an additive function of the error in the estimation of sapwood area based on diameter for each tree in a given patch and the error in the estimation water flux on a sapwood area basis ($g \, cm^{-2} \, h^{-1}$) for the selected trees. For primary and secondary corridor forest, and the riparian forest as a whole, the total error was estimated by averaging the errors across patches.

Micrometeorological Variables

Micrometeorological measurements of the bulk air flowing into the forest canopy were taken at both sites concurrent with sapflow measurements. At both sites, air temperature, relative humidity, and photosynthetic photon flux density (PPFD) were measured at 2.1 m height above the ground on an upper flood-plain terrace which placed the sensors approximately 5 m above the active stream channel where the riparian vegetation was located.

Leaf Area Index

Leaf area index (*LAI*) was estimated using a plant canopy analyzer (LAI-2000, LiCor Inc., Lincoln, NE). *LAI* was calculated for primary and secondary channel patches by averaging the individual estimates of *LAI* at eight points under the canopies of individual trees. Six trees (two in newly established and four in successionally advanced patches) were selected for measurement. Point measurements of *LAI* were made at 3 and 7 m from the base of a given tree in the four cardinal directions. Since *LAI* was estimated under the canopies of selected trees, the measurement of *LAI* is considered relative because no accounting was made for the gap fraction.

Results

In addition to variation in size (canopy area, m^2) and composition of the twelve riparian forest patches (Table 1), there were also differences in structure between patches located on primary and secondary stream channels. Patch canopy areas assessed from aerial photos (Fig. 1) ranged from 462 to 1985 m^2. The percentage of sapwood area per unit canopy area contributed by willow ranged from 0 to 49% among patches. The average diameter of cottonwood and willow trees in patches (weighted by the relative sapwood area contribution of each species to the patch, Fig. 2) was significantly (p=.03) smaller within forest patches located along the primary channel (28 ±4 cm) than in patches located along secondary (54 ±9 cm) channels. Likewise, sapwood area to total canopy area ratios were higher for patches along the primary channel than for patches along secondary channels (Table 1). Generally, fewer willow trees were found in along secondary channels.

Transpiration estimates for individual cottonwood and willow trees were averaged to calculate mean sap flux on a sapwood area basis (J_s) for a given species, for trees located along the primary and secondary stream channels. J_{smax} was calculated for each tree as the mean of the three highest values of J_s over the course of a given day (Fig. 3). J_{smax} for cottonwood was consistently higher for trees along primary stream channels in June (day of year, DOY 158-159) and higher for trees along secondary stream channels in April, July, August, and October (DOY 111-112; 191-193; 223-227; and 285-288 respectively). But, significant differences (p<0.05) between J_{smax} of cottonwood along primary and secondary stream channel were found only in August and October (DOY 224 and 286 respectively). Conversely, J_{smax} for willow was higher for trees along primary stream channels at all time periods except October. There were no days on which J_{smax} of willow trees was statistically different (p<0.05) between trees along primary and secondary channels, although sample size was relatively small (n=2). There were, however, apparent trends in the differences in J_{smax} between trees along primary and secondary stream channels for both species that justified separate calculations for these two patch types.

J_s (g cm^{-2} h^{-1}) for cottonwood and willow is shown in Figures 4 and 5, respectively. For

cottonwood (Fig. 4), maximum rates of J_s were low in April (12-25 g cm^{-2} h^{-1} for primary channel trees

and 28-29 g cm^{-2} h^{-1} for secondary channel trees) when leaves had just reached full expansion. Highest

J_s (37.0 ±1.5 g cm^{-2} h^{-1} for trees on the primary channel and 44.4 ±12.5 g cm^{-2} h^{-1} for trees on

secondary channels) occurred in July when air temperatures and vapor pressure deficit were highest

(data not shown). Lowest maximum J_s (12.5 ±3.2 g cm^{-2} h^{-1} for trees on the primary channel and 29.6

±6.1 g cm^{-2} h^{-1} for trees on secondary channels) occurred in October following a morning frost on day

285. J_s remained low for at least 4 days after the frost event. For both species, there was a reduction

in J_s in August on day 224 when irradiance (PPFD, μmol photons m^{-2} s^{-1}) was low due to cloud cover

(data not shown). J_s for willow was much lower than that for cottonwood in April and October (J_s <15

g cm^{-2} h^{-1} for both patch types) while the highest J_s was observed in June (51.4 ±16.8 g cm^{-2} h^{-1} for

primary channel trees and 31.6 ±5.2 g cm^{-2} h^{-1} for secondary channel trees, Fig. 5). The sapwood area

of all trees fitted with HPV probes was directly measured using increment cores, thus the error reported

in the text above is due to the variance among trees.

An estimate of the daily transpiration of individual trees on a single day (DOY 159) is shown in

Figure 6. The largest cottonwood trees (those greater than 0.5 m in diameter) fitted with sensors were

found to transpire between 200 and 500 liters of water on a typical day. The range in size of willow

trees at Lewis Springs was much smaller than that of cottonwood. Trees fitted with sensors transpired

between 30 and 100 liters of water per day on DOY 159.

The heat pulse velocity sensors used in this study showed strong agreement with temperature

difference probes (TDP) in estimations of transpiration (E) from a cottonwood tree fitted with both

sensor types (Fig. 7). Estimates using the two methods are positively correlated (r^2=0.94, p<0.0001)

and follow the 1:1 line.

Relationships between sapwood area (m^2) and tree basal diameter (m) for cottonwood and

willow are shown in Figure 8. Diameter of cottonwood trees bored for sapwood area estimates ranged

from 16 to 100 cm and sapwood area ranged from 100 to 2100 cm^2. Diameter of willow ranged from

7 to 37 cm, and sapwood area ranged from 25 to 600 cm^2. The curve for both cottonwood (r^2=0.95)

and willow (r^2=0.88) followed a power ($y=m*x^b$) relationship that has been observed in other tree species (Vertessy et al. 1995).

Mean daily transpiration at the canopy scale for all patches in July was 4.8 ±0.7 mm day^{-1} and ranged from 5.7 ±0.6 mm d^{-1} in young forest patches adjacent to the primary stream channel to 3.1 ±0.6 mm d^{-1} in successionally advanced patches on secondary channels (Fig. 9). Diurnal and seasonal patterns of E for trees along primary and secondary channels followed the same patterns as those found for cottonwood and willow separately. Also, mean LAI (m^2 leaf area m^{-2} ground area) was significantly (p<0.0002) higher in patches located on primary channels than along secondary stream channels over the course of the growing season (Fig. 10).

Discussion

Daily transpiration for the cottonwood/willow forest in 1997 along the San Pedro River at the location of the SALSA program measurement campaigns ranged from 1.2 to 4.8 mm d^{-1}. Transpiration rates appear to fall within the range of that found in broadleaf (David et al., 1997) and tropical-dry forests (Granier et al., 1996). These transpiration rates are low compared to that of salt cedar (*Tamarix ramosissima*) stands in similar environments. Salt cedar, a non-native tree, has completely replaced native riparian forest in many areas in western North America (Brotherson and Field, 1987; Busch and Smith, 1995). Sala et al. (1996) and Devitt et al. (1998) reported maximum evapotranspiration rates in stands of salt cedar of 10-12 mm d^{-1}. Even though these estimates include evaporation from the soil surface, and come from a different river system, these rates are more than twice the rate found in cottonwood/willow forst as reported here. This large difference in transpiration has important implications for regional water budgets in areas where salt cedar has the potential to replace, or already has replaced, native riparian species, and gives an indication of the potential effects of salt cedar removal and restoration of native forest.

What may be more significant than average transpiration rates from cottonwood/willow forests is the heterogeneity of transpiration at the patch scale. Cottonwood/willow forest dynamics in the Southwest are strongly controlled by flood disturbance. *Salix* and *Populus* establish on exposed alluvial deposits along active channels (Stromberg, 1993; Stromberg, 1998), but further establishment within these intact forests is limited. As the forest patches develop and the stream changes course, stem densities decline and eventually patches become dominated by just a few large cottonwood and willow individuals. These patches often line the outer margins of the riparian flood plain on abandoned secondary channels (Asplund and Gooch, 1988). Forest dynamics at this scale have large ramifications for evapotranspiration.

Our data show that transpiration per unit ground area declines with successional development of cottonwood/willow forest at the Lewis Springs study site. During the peak of the growing season (June-August), transpiration in young forest patches near the primary stream channel was as much as

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twice that in older patches on outer secondary channels. Admittedly, our estimates of patch transpiration were based on a limited set of trees fitted with sap flux sensors. Cooper et al. (this issue), however, using LIDAR found remarkable agreement with our estimates of the spatial variation in transpiration across the forest stand at the Lewis Springs study site.

Variations in transpiration between patches in this forest were a function of structural differences at that level. Structural differences include the ratio of sapwood area to canopy area (Table 1) and leaf area index (Fig. 10), as well as differences in the transpiration rate per unit sapwood area for cottonwood and willow trees along primary and secondary channels related to tree diameter (Fig. 2). Declines in transpiration with successional development appear to be related to thinning within the stand and reductions in sapwood area and leaf area of the patch rather than reduced transpiration by individual trees. In fact, the larger cottonwood trees located along secondary channels appear to have higher transpiration on a sapwood area basis (J_s, Fig. 4) than cottonwood trees along primary stream channels. Water stress, estimated from predawn and midday water potentials, was not different for trees growing along primary and secondary stream channels at this site (Snyder and Williams, this issue), suggesting that differences in water status are not responsible for the differences in J_s.

Structural differences between younger and older portions of the forest, and the location of these patches relative to the surrounding aridlands can affect tree transpiration. Sala et al. (1996) likewise demonstrated that structural rather than physiological characteristics accounted for differences in stand-level transpiration between salt cedar and native riparian forest. Our results, furthermore, are an example of how population dynamics may determine ecosystem fluxes in these plant communities (Williams et al., 1999). In this case, mortality and lack of regeneration within established forest patches translates into considerable spatial variation in transpiration.

A proportion of seasonal and patch-level variation in transpiration in this study was related to phenological differences between cottonwood and willow and to changes in species composition with patch succession. There was greater variation for transpiration on a sapwood area basis among individuals of willow than among individuals of cottonwood. As a subdominant species, willow may be exposed to a relatively heterogeneous light environment and over the course of a day, is exposed to

differing light levels (Kelliher et al., 1992; Breda et al., 1995; Granier et al., 1996). Consequently, aggregation of transpiration using the sap flow technique may be more difficult for stands or forest patches with high densities of willow.

In this desert riparian forest, however, transpiration from cottonwood contributes proportionally more of the total water flux from the stand than does willow. Cottonwood contributed at least 51%, and on average 85%, of the total sapwood area to individual patches in this study. Furthermore, in contrast to cottonwood, transpiration from willow was negligible in early spring (April) and fall (October). These seasonal differences may be related to differences in leaf phenology and the relative sensitivity of the two species to frost. In April, leaves of willow had only recently begun to expand, and thus transpiration was very low. Cottonwood, however, possessed many fully expanded leaves in April and trees transpired at fairly high rates. The highest transpiration rates occured when temperature and vapor pressure deficit (D) was highest, in this case June and July (data not shown). Transpiration was slightly lower in August perhaps because of the lower radiation input on cloudy days and the generally more humid atmosphere. Toward the end of the growing season, the decrease in transpiration from day 284 to 285 may have been a direct response to nighttime frost, which appears to have reduced transpiration from both willow and cottonwood.

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Table 1.　　Stand structural characteristics for twelve patches of riparian forest vegetation at the Lewis

Springs study site on the San Pedro River in southeastern Arizona. Canopy area, number of stems, and

sapwood area/canopy area ratio are given for patches located along the primary and secondary stream channels.

Canopy area (m^2) refers to the planar projected area of the canopy as seen from aerial photography. Percent

(%) willow refers to the percentage of the total sapwood area that willow contributes to a given patch. Mean

values (and SE of mean in parenthesis) are shown for the structural characteristics of all patches on either primary

or secondary stream channels.

Position	Patch Number	Canopy area (m^2)	Stems		Sapwood area/Canopy area ($cm^2\ m^{-2}$)		
			Cottonwood	Willow	Cottonwood	Willow	% Willow
Primary	1	444	8	14	13.8	7.1	34
	3	643	31	25	15.8	3.9	20
	5	756	4	13	5.0	4.8	49
	6	800	33	43	18.1	2.9	14
	10	1028	58	13	16.4	1.3	7
mean		734(95)	26.8(9.7)	21.6(5.8)	13.8(2.3)	4.0(1.0)	25(8)
Secondary	2	462	2	5	3.9	1.3	25
	4	664	9	20	9.1	2.2	20
	7	814	4	0	6.1	0.0	0
	8	828	12	5	9.7	0.1	1
	9	997	2	8	4.6	0.3	5
	11	1421	13	7	9.8	0.9	8
	12	1985	41	1	17.9	0.2	1
mean		1021(196)	11.9(5.2)	6.6(2.5)	8.7(1.8)	0.7(0.3)	9(4)

Figure Captions

Figure 1. Aerial view of the Lewis Springs study site on the San Pedro River in southeastern Arizona. The image depicts the location of the forest patches selected for comparisons of transpiration on primary (solid line) and secondary (dashed line) stream channels.

Figure 2. Structural characteristics for forest patches on primary and secondary stream channels at the Lewis Springs study site on the San Pedro River in southeastern Arizona. Mean tree diameter at 1.35 m height (mean tree diameter is the weighted average for both cottonwood and willow trees based on the respective sapwood area contribution of each species within a given patch). The means were significantly different (p=0.03).

Figure 3. Mean maximum daily sap flux on a sapwood area basis (J_{smax}, g cm^{-2} h^{-1}) for cottonwood (*Populus fremontii*) and willow (*Salix goodingii*) trees along primary (solid symbol) and secondary (open symbol) stream channels at the Lewis Springs site in 1997. Statistically significant differences ($p<0.05$) between J_{smax} of trees on primary and secondary channels (day of year, DOY 224 and 286 for cottonwood) are denoted by '*'.

Figure 4. Mean sap flux on a sapwood area basis (J_s, g cm^{-2} h^{-1}) for cottonwood trees (*Populus fremontii*) located on primary and secondary channels at the Lewis Springs study site on the San Pedro River in southeastern Arizona. Measurements were taken for a total of 21 days during five key periods during the growing season in 1997.

Figure 5. Mean sap flux on a sapwood area basis (J_s, g cm^{-2} h^{-1}) for willow trees (*Salix goodingii*) located on primary and secondary channels at the Lewis Springs study site on the San Pedro River in southeastern Arizona. Measurements were taken for a total of 21 days during five key periods during the growing season in 1997.

Figure 6. Daily cumulative sap flow (L d^{-1}) of the 9 cottonwood (*Populus fremontii*) and 6 willow (*Salix goodingii*) trees fitted with sap flow sensors at the Lewis Springs study site on DOY 159, 1997.

Figure 7. Comparison of heat pulse velocity (HPV) and temperature difference probe (TDP) estimates of transpiration. Measurements were conducted on one cottonwood tree over a 24-h period at the Lewis Springs site in June, 1998.

Figure 8. Relationship between sapwood area (SWA, cm^2) and tree diameter at 1.35 m (DBH) for cottonwood (*Populus fremontii*) and willow (*Salix goodingii*) at the Lewis Springs study site on the San Pedro River in southeastern Arizona. Regression analyses yielded a power relationship with $r^2 = 0.95$ for cottonwood and $r^2 = 0.88$ for willow.

Figure 9. Mean transpiration on a canopy area basis (E, mm h^{-1}) for patches of riparian vegetation located on primary and secondary channels at the Lewis Springs study site on the San Pedro River in southeastern Arizona. Measurements were taken for a total of 21 days during five key periods during the growing season in 1997.

Figure 10. Mean leaf area index (LAI, leaf area m^2 ground area m^{-2}) for patches of riparian vegetation located on primary and secondary stream channels at the Lewis Springs site in 1997. Error bars represent the standard error of the mean (SE).